An Assessment of Information Pertaining to the Status of Trumpeter Swans (*Cygnus buccinator*)

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INTRODUCTION

The trumpeter swan (*Cygnus buccinator*) is the largest native waterfowl species in North America. Historically, their annual range likely encompassed most of Canada and the United States south of tundra areas (Gale et al. 1987), and they probably were much more numerous than they are today. However, no good estimates of abundance exist for any region of North America prior to the 1930s. Their abundance and regional extent may have resulted in a rather contiguous distribution of the species. Reports from the Hudson's Bay Company indicate that thousands of swan skins (both trumpeter and tundra [*C. columbianus*] swans) were shipped to London markets annually during the 1800s (Banko 1960). Probably due to the take of trumpeters for markets and subsistence, trumpeter abundance was reduced throughout the continent, and ranges of breeding and wintering aggregations became compressed. In the early 1900s, a small group of swans inhabiting the region where the borders of Montana, Idaho, and Wyoming converge was believed to be the only free-ranging group of trumpeters remaining. Many people feared the species was on the verge of extinction. With the advent of aerial waterfowl surveys, which greatly expanded the area of the continent that could be searched, additional aggregations of breeding trumpeters were discovered in Alaska and Canada in the mid-1900s. Although these additional groups of birds brought the total number of trumpeter swans only to a few thousand, their discovery allayed fears of the imminent extinction of the species. Today, major breeding aggregations exist in only a few regions (Mitchell 1994), but extensive reintroduction efforts have established additional breeding flocks of trumpeters in areas believed to have been inhabited historically.

No subspecies of trumpeter swans are recognized. However, the trumpeter, along with the whooper (*C. cygnus*), tundra, and Bewick's (*C. bewickii*) swans comprise a close-knit evolutionary complex called the northern swans (Johnsgard 1978). The relationships among these taxa are far from clear. Some have regarded the trumpeter as a subspecies of *C. cygnus* (Delacour 1959, Johnsgard 1974, Cooper 1979), whereas Banko and Schorger (1976) suggested that whooper and trumpeter swans comprise a superspecies. Barrett and Vyse (1982) examined the genetic relationships among trumpeter, tundra, trumpeter-tundra hybrid, and mute swans *(C. olor*). Although their sample sizes were small, their analyses revealed no differences between trumpeter swans, tundra swans, and the trumpeter-tundra hybrids, suggesting a 'close taxonomic relationship' between trumpeters and tundra swans. Meng and Parkin (1993) determined that DNA fingerprints of Bewick's, trumpeter, and whooper swans suggested a close relationship to one another. Trumpeter swans interbreed with whooper, tundra, Bewick's, and mute swans (Banko and Schorger 1976). Crosses between trumpeter and tundra swans are fertile (J.G. King, pers. comm. *in* Mitchell 1994). Pairs of trumpeter-tundra hybrids have successfully fledged offspring in captivity, as have pairings of trumpeter-tundra hybrids with trumpeter swans (Sladen et al. 2001).

Over the years, several popular articles have stated that trumpeter swans were once endangered, and only recently were removed from the endangered species list. Undoubtedly, if the Endangered Species Act had been in place during the early 1900s, trumpeter swans would have been listed due their low abundance at that time. However, trumpeter swans were never listed as

endangered or threatened in the U.S., and the Canadian federal government does not have legislation analogous to the U.S.'s Endangered Species Act. The trumpeter swan was listed in the U.S. Fish and Wildlife Service's (Service) 'Red Book' during the 1960s, due to a limited understanding of its status at that time. The Red Book is developed under the auspices of the International Union for the Conservation of Nature, and is an international compilation of globally threatened or endangered species. However, trumpeter swans are not on the most recent 'Red List' in either Canada or the U.S. (Stattersfield and Capper 2000). The trumpeter swan also has been on the Service's list of 'Species of Management Concern' in the past, although it is not on an updated list (Birds of Conservation Concern) that currently is being finalized (S. L. Jones, pers. comm.). In 1989, the Service was petitioned to list a portion of the trumpeter swans (Rocky Mountain Population, see below) as threatened. However, the petition presented information that was deemed insufficient to warrant they be listed (55[81] Federal Register 17646-17648, April 16, 1990). In Canada, the trumpeter swan was listed as a vulnerable species in 1978 (Mackay 1978). After a status assessment conducted in the mid-1990s, the Canadian federal government moved the species to its 'not at risk' category (COSEWIC 2002). However, in Alberta it is listed as a 'vulnerable' species (Government of Alberta 2002), which means that without management and protection the species could become threatened or endangered *within the province* (emphasis added).

As mentioned previously, the historical abundance and range of trumpeters suggest a generally contiguous distribution of the species, likely with a fair amount of mixing of birds from various regions. As their range was restricted due to overexploitation and habitat loss, remnant groups of birds inhabited relatively disjunct breeding areas. Ecologists use the term population size very loosely to pragmatically define assemblages of individuals of one species (Ricklefs 1979:507). Recently, trumpeter swans were divided into 3 'populations', based on areas in which they nest. These populations are defined primarily for management purposes and not in recognition of reproductive isolation or genetic differentiation (Trost et al. 2000). In fact, one of the populations is derived almost exclusively from birds and eggs translocated from the other 2 populations. Although demographic differences may exist among these groups (e.g., slight differences in egg production and hatchability), to date information from monitoring and research programs has led biologists and managers to conclude that differences are not large. The Pacific Coast Population (PCP) is comprised primarily of birds that nest in Alaska and winter along the west coast of Canada and the U.S. as far south as Oregon (Fig. 1). Observations of a very limited number of marked birds from this group suggest that birds nesting in Alaska do not often migrate or winter east of British Columbia or the Pacific Coast states. The Rocky Mountain Population (RMP) is comprised of birds that nest east of the range of the PCP to areas just east of the western border of Saskatchewan and points south. Most birds in the RMP winter at the confluence of the borders of Montana, Idaho, and Wyoming (hereafter termed the 'tri-state' area). The Interior Population (IP) is comprised of birds that nest east of the range of the RMP. The IP is the result of extensive restoration efforts, and is composed exclusively of PCP and RMP birds and eggs that were translocated to these eastern areas. Birds from the IP winter primarily in areas south of their nesting grounds.

The status of the trumpeter swan is officially assessed at 5-year intervals, and the most recent survey (2000) resulted in a count of 23,647 swans (Caithamer 2001). This represents a 535% increase in the total number of trumpeter swans since 1968 (the first year of the survey), or an average growth rate of 5.9% per year. Respective values for the PCP (516%, 5.8% per year), RMP (352%, 4.8% per year), and IP (3,697%, 12.0% per year) suggest all populations are increasing at fairly high rates.

Of all the populations, the status of the RMP has been subject to the largest amount of debate over the years. The RMP is comprised primarily of 2 groups of birds, one that nests in Canada (Canada Flocks) and the other that nests in tri-state area (Tri-state Area Flocks). The latter group contained only about 70 birds in the early 1930s, and these were erroneously thought to be the only free-ranging trumpeter swans in the world. The birds nested primarily in Yellowstone National Park and the Centennial Valley area of Montana, and wintered in those areas and adjacent areas in Idaho. To further protect these swans, the U.S. government acquired land in the Centennial Valley in 1935 and established the Red Rock Lakes Migratory Waterfowl Refuge (now National Wildlife Refuge [NWR]) 'principally for the perpetuation of this species' (Banko 1960:40). This area encompassed much of the known remaining nesting range for swans in the region. Many management activities were initiated upon establishment of the refuge. These included a survey program to monitor status of the birds, restricting human activities to decrease disturbance, limiting grazing, providing winter feed for the swans, predator control, and curtailing muskrat trapping (muskrat lodges were the main source of nesting sites). Although the number of swans in the Centennial Valley increased during the next 2 decades, in the 1950s their abundance seemed to stabilize at around 500-600 birds. Because these birds share winter areas with the RMP swans that nest in Canada, a few conservation groups are concerned that the trumpeter swans nesting in the tri-state area could be outcompeted for limited resources by their Canadian counterparts, or experience substantial winter mortality due to severe winter weather. Hence, the groups have petitioned the U.S. Fish and Wildlife Service to list the Tri-state Area Flocks as threatened or endangered under the Endangered Species Act (The Biodiversity Legal Foundation and Fund for Animals 2000).

The remainder of this document will review data from monitoring programs designed to assess the status of trumpeter swans. The analyses will focus on the status of the RMP and its various nesting components.

ABUNDANCE

North American Total Trumpeter Swans

The status of trumpeter swans (including all recognized populations) is officially assessed using a periodic, range-wide survey (Trost et al. 2000:64). This survey was first conducted in 1968, and since 1975 has been conducted at 5-year intervals. The results of this survey indicate that trumpeter swans (all 3 populations combined) have increased from 3,722 birds in 1968 to 23,647 birds in 2000 (Caithamer 2001), an average increase of 5.9% per year (Fig. 2).

Rocky Mountain Population

The RMP is generally agreed to be comprised of 3 aggregations of birds. The terminology for these groups has varied over time, having been called populations, subpopulations, segments, and flocks. Recently, the FWS has adopted the term 'flock' to designate these aggregations, because (1) they believe that extant information is insufficient to determine which term is most appropriate, and (2) they desired consistency in terminology between the FWS and the Pacific Flyway management plan for RMP trumpeter swans (U.S. Fish and Wildlife Service 2001:9). Thus, the 3 groups that collectively constitute the RMP are: (1) the Canada flocks, (2) the Tri-state Area flocks, and (3) restoration flocks. The Canada flocks consist of birds that nest in portions of Saskatchewan, Alberta, southwestern Northwest Territories, southeastern Yukon Territory, and northeastern British Columbia. The Tri-state Area flocks nest primarily in northwestern Wyoming, eastern Idaho, and southwestern Montana. The restoration flocks consist of birds derived primarily from adults and cygnets that were translocated from the Tri-state Area flocks to various refuges and wildlife management areas in attempts to establish new nesting groups (see Gale et al. 1987 for further discussion of translocation efforts). Primary restoration flocks designated as RMP birds exist at Ruby Lake NWR and in Oregon (Malheur NWR and Summer Lake Wildlife Management Area). Swans from the Canada and Tri-state Area flocks winter mostly in the tri-state area, whereas restoration flocks tend to winter in locales near nesting grounds. Unless otherwise stated, analyses will include data from only the Canada and Tri-state Area flocks.

The 5-year periodic survey indicates that the RMP as a whole (restoration flocks included) increased from 811 birds in 1968 to 3,666 birds in 2000 (Caithamer 2001), an average increase of 4.8% per year. If restoration flocks are excluded from analyses, the average rate is 5.5% per year (i.e., the abundance of swans in restoration flocks has declined from 1966-2000).

Additionally, annual midwinter surveys have been conducted in the tri-state area to assess the status of the entire RMP. Variation in survey responsibilities and survey effort prior to 1972 resulted in information that was not comparable from year-to-year. Beginning in 1972, the U.S. Fish and Wildlife Service took the responsibility of coordinating the survey, and better standardized the survey protocols. However, between 1972 and 1981, the survey area was expanded, which impacted the ability to assess results. Since1981, survey coverage has been reasonably consistent and has included essentially all known wintering areas of the RMP. Therefore, the 1981-present data are probably most appropriate time-series for an assessment of trend. Unfortunately, an unknown number of tundra swans may be included in the counts. Tundra swans have been observed in the survey area (Gale et al. 1987), and the two species cannot reliably be distinguished during aerial surveys. Thus, the midwinter counts may be biased high. If we assume, however, that the proportion of tundras swans relative to trumpeter swans in the midwinter survey have not increased substantially over time, the midwinter counts may provide a reasonable index to the growth of the RMP. Given these caveats, the midwinter survey suggests an RMP size of 4,360 swans in 2002 (Olson 2002), and an increase of approximately 5.3% per year during 1981-2002 (Fig. 3).

Canada Flocks.– Annual fall surveys for these flocks have been conducted since 1959. Efforts are focused on the group of birds that nest in the Grande Prairie region; thus, the survey does not represent a comprehensive account of all RMP swans nesting in Canada. Although data in Gale et al. (1987) suggest the majority of swans are contained in the Grande Prairie flock, a substantial and growing number of swans nests in the Northwest Territories (Shandruk 1990, G. Beyersbergen, pers. comm.). As mentioned previously, a midwinter survey of all swans in the tri-state region is conducted annually, and is thought to provide abundance estimates for the entire RMP. If we assume that mortality of swans counted in the tri-state region in the fall (i.e., U.S.-nesting birds less those in restoration flocks) and their movement out of the region is negligible between when they are counted in fall and the midwinter survey (or at least are a relatively constant proportion of the fall counts), subtracting the fall count from the total midwinter count may provide a reasonable index to changes in the numbers of birds in the Canada flocks. Using this method, the Canada flocks appear to have increased by approximately 7.3% per year since 1981 (Fig. 4). Interestingly, the growth rate for the Grande Prairie flock also was 7.3% per year from 1966-88, but the counts suggest the growth rate has been 1.0 (i.e., stable abundance) since then. G. Beyersbergen (Canadian Wildlife Service, pers. comm.) explained that counts in the Grande Prairie region were extensive and probably enumerated most birds until 1996, after which survey effort was curtailed. Thus, if the estimate for the size of the Canada flocks obtained by taking the difference between the fall and winter counts is reliable, contemporary growth probably is the result of expansion of flocks outside of the Grande Prairie survey area.

Tri-state Area Flocks.– These flocks have been the most intensively surveyed portion of the RMP. Fall surveys were initiated in the 1930s and have continued to the present. Of course, survey methods and coverage have changed during that time. From the initial surveys until 1945, the surveys were conducted by ground crews who attempted to locate all major nesting sites in Yellowstone National Park, the Centennial Valley, Montana, and nearby areas. Beginning in 1946, aerial crews surveyed the region, which expanded the range of the survey, primarily by locating more remote nesting areas that were not easily accessed by ground crews. Between 1946 and 1965, as the number of swans expanded and translocation efforts to develop restoration flocks intensified (Gale et al. 1987:425-426), the area of the survey continued to expand. By 1966, most areas in the tri-state region containing nesting trumpeter swans were identified, and the coverage has remained relatively consistent since then (D. Olson, pers. comm.). Interestingly, however, when the fall counts of the tri-state birds are plotted over time, there do not appear to be significant jumps between periods when survey methods changed (e.g., between counts for 1944 and 1945 vs. counts for 1946 and 1947, Fig. 5). Rather, the points on either side of these transition times suggest a smooth line. Thus, it is possible that even the ground counts, limited as they were, did a good job of enumerating the swans that existed during the 1930s and early 1940s. We cannot definitively state that the increase in swan numbers during the 1930s to 1950s represented true population growth, because changes in survey methodologies and coverage are confounded with the increase. However, recall that winter feeding of swans began in 1935, and managers believed that the supplemental feed improved the body condition of the swans and improved survival (Gale et al. 1987:233-238), and Gale et al. (1987) noted a negative correlation between mortality and the amount of grain fed to swans during winter. Therefore, the

increases seen between the 1930s and the 1950s are quite possibly real and not simply an artifact of changing survey protocols.

We wanted to investigate trends in abundance over time using regression methodologies. However, regression results can be greatly influenced by beginning and end points of the time series. Because we could not visibly discern any abrupt changes near the years where survey changes were made (e.g., changing from ground-based to aerial surveys), we used all of the information during early years of the survey in regressions. However, during the late 1980s, managers enacted several rather dramatic management actions. Hazing of swans within their primary winter range and translocations of birds to other wintering sites were intensified in an attempt to disperse them to other areas and develop migratory pathways to additional wintering sites (Shea and Drewien 1999). Also, the 67-year practice of providing winter feed to swans was terminated during the winter of 1992. Therefore, we excluded data after 1988 from regression analyses.

The plot of annual estimates suggested a possible change in rate of growth at some time during the early 1950s (Banko 1960). Therefore, we decided to use piecewise regression (e.g., Neter et al. 1985), and varied the 'breakpoint' (i.e., year) where slopes of the regression lines changed. We then selected the model with the lowest coefficient of variation (R^2) as that which best fit the data. Results for the tri-state birds (all cohorts) suggested a change in growth rates after 1953 (Fig. 5). Prior to that time, swan counts increased at a rate of 8.8% per year ($P < 0.01$). Abundance declined slightly (0.5% per year) from 1954-1988 ($P[\beta<0] = 0.03$, $R^2 = 0.22$). If only the data from 1966 (i.e., the first year in which biologists believe survey coverage and protocols were fairly standardized) to 1988 are included in analyses, the data suggest a slight ($\beta = -0.7\%$) but not statistically significant ($P[\beta < 0] = 0.19$) annual decrease. Counts appeared to decline more sharply after 1988, and particularly between the 1992 and 1993 counts, coincident with the termination of winter feeding. Managers predicted a decline in abundance with the cessation of feeding (which occurred in conjunction with other disruptive management actions, including hazing and translocation of swans), although the predicted magnitude was uncertain (Trost et al. 2000:64). At its lowest point after 1988, the number of swans (277) was 57% below the peak of 651 birds in 1954, and 49% below the 1954-88 mean abundance (543 birds). However, abundance increased at 3.6% per year during 1993-2001 ($P[\beta>0] = 0.02$, $R^2 = 0.63$), and by 2001 was only 22% below the 1954-88 mean. Trends for white birds (i.e., adults and subadults) were virtually identical to those for total birds (Fig. 5).

Results also suggest that the decline in tri-state swans during the mid-1950s to 1988 was evident only in Montana- and Wyoming-nesting birds (Figs. 6, 7). Swan abundance in both of these states declined at approximately the same rate (0.6 - 1.0% per year, $P \leq 0.1$). The decline in abundance during 1989-92 was most dramatic in Montana. Although the number of swans has increased dramatically since 1992 (7% per year, $P < 0.01$), the 2001 count was 58% below the 1953-88 average. Since 1992, no trend has been evident in the counts of swans in Wyoming ($P = 0.42$), and the count in 2001 was 12% higher than the 1956-88 mean. The number of birds in Idaho continued to increase throughout the entire historical record, albeit at a slower rate after

1961 than prior to that year (Fig. 8). In Idaho, the 2001 count was the second highest recorded and was 73% higher than the 1961-88 average. The distribution of nesting birds in the tri-state region also apparently has changed over time. In recent years, the proportion of birds counted during the fall survey in Wyoming and especially Idaho has been greater than in earlier years (Fig. 9).

Banko (1960) was perhaps the first to notice that the number of swans nesting in the tri-state region leveled-off in the 1950s. Cygnet production was inversely related to swan abundance, and suggested that the birds had become habitat-limited at that point (Banko 1960). However, we also must realize that winter feeding occurred during this entire period, perhaps artificially increasing carrying capacity above that which occurred naturally. The number of swans in Montana in 2001 was far below levels seen earlier. Nonetheless, recent surveys suggest swan abundance is increasing in Montana. If the rate of growth is maintained, the number of swans in Montana will reach 1953-88 levels in approximately 13 years.

Restoration Flocks.– Two important groups of birds that resulted from translocation activities are officially included in RMP. The Oregon flock is comprised of birds nesting at Malheur NWR and Summer Lake WMA, and the Nevada flock is made up of birds nesting at Ruby Lake NWR and in nearby valleys. The birds at Summer Lake WMA and vicinity came from both Red Rocks Lake and Canada stocks, whereas swans at Malheur and Ruby Lakes NWRs were derived from birds translocated from Red Rocks NWR. The Oregon flock has been surveyed in the fall since 1958. Swans in the Nevada flock has been surveyed since 1971. Overall, the growth of the flock in Oregon has increased ($\beta = 0.008$, $P [\beta > 0] = 0.07$), although the coefficient of determination for the regression ($R^2 = 0.10$) is very low (Fig. 10). The growth of the Nevada flock has shown no trend ($P = 0.43$), although the counts tend to have increased over time.

Yet another group of nesting swans exists in southern South Dakota, northeastern Wyoming, and western Nebraska. This group is known as the High Plains flock, and are descendants of birds that were transferred from Red Rock Lakes NWR to Lacreek NWR during 1960-62 (Monnie 1966). This group of birds has been increasing ($P < 0.01$) at a rate of 3.1% per year since 1980 (Fig. 10), and currently contains 385 birds (R. Kraft, unpub. data). Although this group of birds is assigned to the IP, they were derived from tri-state birds. Some birds from Canada share the same wintering areas as many of these birds (Kraft 2000), but there is no information to suggest the Canadian and High Plains birds have interbred. Thus, the High Plains birds should have remained genetically similar to the tri-state birds, a position supported by some empirical data (Pelizza, unpub. ms.). Using the above arguments, if the numbers for these 3 nesting groups of birds (exclusive of the Summer Lake WMA birds, which have a mixed Tri-state Area/Canada lineage) are added to those for the birds nesting in the tri-state area, the total number of birds derived from tri-state stocks was 697 for 2001 (Fig. 11), or 7% higher than the peak number of tri-state nesting birds.

GENETICS STUDIES

Several studies have been conducted to investigate genetic similarities among different groups of trumpeter swans nesting in North America (Barrett and Vyse 1982, Marsolais and White 1997, Pelizza, unpub. ms.). However, to date only one of those studies has been accepted for publication in a peer-reviewed professional journal. Barrett and Vyse (1982) compared blood proteins among birds from Alaska (PCP), Red Rock Lakes NWR (tri-state nesting RMP), and Grande Prairie (Canada-nesting RMP) swans. Although all 3 groups of swans shared a common allele for all loci surveyed and the mean heterozygosity of the 3 groups was not different, the Alaskan birds possessed alternate alleles at several loci, suggesting that group may differ somewhat from the Grande Prairie and Red Rock Lakes birds. The genetic distance among the 3 groups was identical, indicating a close genetic relationship among them, and led the authors to conclude that the groups sampled were 'virtually identical based on the index of genetic distance.'

Marsolais and White (1997) studied band-sharing coefficients (BSCs) of birds sampled from the PCP, RMP (both tri-state and Grande Prairie nesting birds), and the IP (Ontario flock, comprised of translocated birds from mixed PCP/RMP lineages). They found that the IP and RMP birds had much higher BSCs than those of PCP birds, suggesting less genetic diversity in the former 2 groups. They hypothesized that the low genetic diversity could have been the result of these groups experiencing population 'bottlenecks'. That is, as the range of the trumpeter swan decreased in the 1800s, the few spatially disjunct groups that remained established were composed of birds with similar genetic traits. However, as the listing petition (Biodiversity Legal Foundation et al. 2000:7-8, quoting Marolais 1994) stipulates, 'the fact that the tri-state and interior Canadian populations did not have significantly different mean BSCs, suggests that the tristate population is not less genetically variable than the interior Canadian population.' They go on to state that genetic differences may exist and could be detected using other techniques. However, subsequent studies to address this latter contention were not conducted.

Pelizza (unpub. ms.) studied allele frequencies among birds sampled from the PCP, tri-state nesting birds, and the High Plains flock of the IP. His results suggested some differences between the PCP birds and those from the latter 2 groups, but that birds from the tri-state area and the High Plains flock were essentially identical. He did not collect samples from the Canada flocks.

Thus, although several studies have been conducted, only one has examined directly the relationship between the Canadian and U.S. nesting segments of the RMP. Although that study suggested no differences between the groups, the methods used (starch gel electrophoresis) are dated compared to contemporary techniques using mitochondrial DNA and microsatellites. Thus, Oyler-McCance and Quinn (2001) have initiated a study to better assess potential differences among the 2 groups of birds. This current study should document the extent of interchange between the Canadian and Tri-state Area flocks of the RMP. The proposed

techniques recently have been used to distinguish among sage grouse populations (Oyler-McCance and Quinn 1999).

INFORMATION FROM BANDING/MARKING PROGRAMS

Analysis of mark/recovery data is a complex issue. There are many programs now available to allow investigators to assimilate and analyze data from marking programs. However, results from all analyses are contingent upon the assumptions made by the investigators regarding the quality of the data provided (Brownie et al. 1985). Thus, results from several investigators may vary even though they use the exact same data sets. Unless the assumptions are stated explicitly a priori, one cannot judge the relative value of results. In the following analyses, we subscribe to the assumptions detailed by Brownie et al. (1985), with the exception that the fate of an individual may not be independent of others (e.g., some entire swan families are banded, and because they tend move as a group, their fates are not independent). We have kept the analyses fairly simple, describing primarily resighting locations of swans relative to locations at which they were banded. Because the petition to list the Tri-state Area flocks voices a particular concern that swan hunting seasons in Utah and Nevada are limiting the expansion of tri-state birds to portions of their former range, we provide information regarding occurrences of marked swans in those states.

Marking of migratory birds has been ongoing since the 1920s. As of September, 2000, the Bird Banding Laboratory (BBL) of the U.S. Geological Survey files had 7,374 records of banded trumpeter swans dating back to 1941, yielding 1,936 subsequent encounters of those birds. Additionally, several marking programs using neck colors, patagial tags, and other markers have been conducted over the years, primarily to investigate movement patterns of swans. However, a simple tally of the number of marked and resighted birds may not be appropriate to assess how much data are available for analyses of particular issues. Many of the birds that have been tagged and monitored over time have been manipulated in some way. Some have been translocated to areas far from their capture sites, some have been hand-reared, some are sick or rehabilitated, etc. Obviously, these events have the potential to alter the demographics of the birds. Thus, when biologists wish to make inferences about free-ranging, unmanipulated birds, they tend to use only information from normal, wild birds (i.e., status code 3 of the Bird Banding Laboratory). We would expect these birds to behave 'normally', assuming that the marker used (e.g., legband, neck collar) and handling of the birds do not negatively impact them. By using only these birds, the number of bandings and subsequent encounters can diminish rapidly. For example, of the original 7,374 bands and 1,936 encounters of trumpeter swans, if we restrict the sample to only those birds that are classified as normal-wild, which were banded in the general range of RMP birds, and were banded during the spring and summer (May to September, to ensure we are examining birds from specific breeding locales), the sample of banded birds drops by 71% to about 2,200 birds. The encounters of that specific group of birds drops by 82% to about 370. If we were to subdivide the data even further to look at age- and gender-specific results, usable sample sizes would be reduced even further. Thus, although many swans have been banded and

resighted over the years, when questions pertaining to particular groups of birds are broached, the samples are much less than one might think.

To examine the movements of RMP trumpeter swans using the BBL band-recovery files, we decided to use only those classified as normal-wild and marked on their nesting territories (i.e., banded during May - September). We assumed these birds were most likely to represent 'natural' movement patterns. By restricting the data in this fashion, our banded sample consisted of 1,971 swans (1,420 banded in the tri-state area, and 551 in Canada excluding Saskatchewan [14 birds]) spanning the years 1949-1998 (Fig. 12a). These values resulted in only about 2-6 swans banded per area and cohort per year, on average, and illustrate the small sample sizes available once data are partitioned to account for area, age, and gender effects. The lack of banding data has hindered efforts to estimate vital rates for trumpeters over the years (Anderson et al. 1986, Shea and Drewien 1999:27). Further, only 39% were fitted with some sort of marker (e.g., neck collar, radio transmitter, patagial tag) that would facilitate collection of multiple resighting information, compared to just a leg band.

Only 316 (16.0%) of the 1,971 birds subsequently were encountered (Fig. 12b), and only 5 (0.3%) were encountered more than once. Overall, 60 (3.0%) of the birds were shot or found dead during the hunting season (presumed killed by hunters, although other causes of mortality cannot be ruled out). Of the birds banded in the tri-state region, only 5 were encountered in Utah and Nevada (3 [0.2%] were shot or found dead during the hunting season). In contrast, 3 of 551 birds (0.5%) banded in Canada were recovered in Utah and Nevada (all were shot or found dead during the hunting season). Drawing population-level inferences from such sparse data is not recommended. However, using these crude measures, trumpeter swans from Canada may be approximately 2.6 times as vulnerable to hunting in Nevada and Utah than tri-state birds (i.e., about 1 of every 4 swans shot in Utah and Nevada are of tri-state origin, on average). Also, these data suggest the movement rate of Canadian RMP birds to Nevada and Utah is about 1.5 times that of tri-state nesting swans, although natural transition rates to Nevada and Utah for both groups appear to be very low (< 0.1%).

For comparative purposes, we looked at the data from marked birds that were either translocated to a site distant from the area in which they were trapped (Canada or the tri-state area), or were hand-reared. We combined data from birds that were translocated during the summer (May - September) and winter (October - March). The BBL files indicate that 514 birds met these criteria, and 51 resightings of these birds were noted. Of the resightings, 15 were birds that were shot or found dead, representing 2.9% of the banded birds. Note that this rate is virtually identical to that for birds presumed to be exhibiting 'natural' movements. Further, only 2 (0.39%) of the translocated birds were shot or found dead in Nevada and Utah, compared to 0.3% (6/1,971) of the birds that were banded during summer but not translocated. These results (with the caveat of very small sample sizes) suggest that hunting seasons, at least in Nevada and Utah, are not resulting in much greater harvest rates of translocated swans relative to normal-wild swans.

One other substantial data set available for RMP birds is the neck-collar database maintained by the Southeastern Idaho Refuge Complex (S. Bouffard, pers. comm.). Although the database currently contains approximately 21,000 observations on 1,922 marked birds, the span of years encompassed by the database is relatively short (i.e., 1988-2002), and not all resightings can be associated with individual birds (i.e., not all of the collar information is available in some cases). Also, the data set is comprised of many entries of birds resighted over short time intervals. Thus, this database has similar shortcomings as the band-recovery database maintained by the BBL; once the data are screened to provide information for specific questions, the amount of useful data typically is much reduced. Further, results from studies of neck collar observations are influenced greatly by the amount of effort expended to observe collars. If efforts are not equal or consistent over time and space, inferences regarding movements and other parameters of interest are at best limited. We tried to limit the amount of bias that may occur by reporting general movements of entire groups of marked birds (e.g., all birds banded in summer and released at the same site, all birds banded during winter and translocated to another site), rather than focus on the movements of a small group or a few individuals. However, because levels of observer effort were not available for our analyses, we suggest the reader view the results below with caution.

In this data set, no status code exists analagous to the one in the band-recovery data set that allows us to ascertain the status of the bird when captured (e.g., translocated, hand-reared). Thus, to again attempt to investigate movements of normal-wild birds, we chose to select only birds in which the release site was the same as the capture site, those which were marked on nesting areas, and where the date of release was the same as the date of capture. This reduced the sample to 271 banded birds for which resighting data were possible, and of these, only 157 were fitted with neck collars. These birds were marked at Red Rock Lakes NWR (155) and Gray's Lake NWR (2) (Fig. 13a). The encounter locations (1,563) for these birds were almost entirely within the tri-state area, with the exception of 1 bird sighted in Alberta (Fig. 13b). That bird was a subadult male marked in July of 1990 at Red Rock Lakes NWR and was sighted numerous times in the tri-state area. The sighting in Canada occurred in May of 1992, and it was subsequently seen alive once more in December of 1992 in Montana. It died of unknown causes in Montana during March 1993.

One hundred and ninety-nine swans were captured during summer in the U.S. and translocated to distant release sites. Collectively, those birds were resighted 903 times, and 791 (88%) of the observations were in the tri-state area (Fig. 14a). One bird that was captured at Malheur NWR and released at the Summer Lake Wildlife Management Area in Oregon was resighted in Utah, constituting the only sighting of a summer-translocated bird in that state. Of the birds that were captured during the winter in the U.S. and translocated to another location, 78% of the subsequent observations occurred in the tri-state area, and only 2.3% occurred in Utah and Nevada (Fig. 14b). If birds that were shot during an experiment in which swans were captured in Idaho and released *during the hunting season* at Bear River Migratory Bird Refuge are deleted (all of the birds were shot within a few weeks of being translocated, several within just a few days), 87% of the birds seen in those states during or immediately following the hunting season

apparently are still alive. In both types of translocations (summer or winter), however, most subsequent observations of birds were in the tri-state area..

DISCUSSION

Although a fairly large amount of data exists regarding trumpeter swans, arguably much of it has not been collected in a manner amenable to analyses that would allow strong inferences from results. Operational monitoring programs (e.g., leg-banding), so important for assessment of the overall status of birds and other animals, largely has been conducted either opportunistically or without a sound sampling design (e.g., Anderson et al. 1986, Shea and Drewien 1999:27, Bouffard 2000). Often, treatments changed over time or several treatments were attempted concurrently. Although these efforts were done with a desire to do what was best for swans, treatment effects often were confounded, and precluded identification of effective management actions. Many of the arguments used to influence trumpeter swan management over the years have been based on results and conclusions from studies that remain unpublished in peer-reviewed scientific journals. In many cases, conclusions are advanced that we feel are unsupported by the data. Although causes for why the reports were not published may be varied, a possibility is that the studies lacked the scientific rigor needed to support conclusions.

An exception to the above statements concerns the count surveys that have been conducted, including the 5-year survey of all trumpeter swans and those conducted during various portions of the year for specific aggregations of birds. Although these efforts, too, have been impacted somewhat by changes in methodology and survey coverage over time, we believe those impacts to be minimal. However, the counts are not true censuses of the swans, and each count therefore contains some unknown and unmeasured variance associated with the sampling procedure. Thus, the best use of the data is to assess trends over time, rather than treat counts as being measured without error and comparing specific counts to each other.

The information from the swan surveys suggest the RMP as a whole has been increasing at a modest rate. Further, after a sharp drop in abundance following the cessation of winter feeding, intensification of translocations, hazing of birds from primary wintering sites, and other activities during the late 1980s and early 1990s, the number of tri-state birds has increased since 1993. The most recent count of tri-state birds (421) is only 22% below the 1954-88 average, a time when the carrying capacity of the landscape perhaps was higher due to feeding of grain to swans. Interestingly, the area that exhibited the greatest drop in abundance after the aforementioned management actions were enacted was Montana, whereas the number of swans in Wyoming and Idaho currently are at or near record highs. Abundance in Montana dropped well below the average observed during the 1950s-80s, and has not yet returned to values near those experienced immediately prior to the management actions. Thus, one could speculate that overall swan habitat has not improved dramatically over time. Results from some monitoring and investigations suggest that foods believed to be preferred by swans (e.g., *Elodea canadensis*, *Potamogeton* spp.) have decreased in abundance over time in areas of Red Rock Lakes NWR (e.g., Paullin et al. 1987, Gale et al. 1987). Other species, such as *Myriophyllum exalbescens* and

Ceratophyllum demersum appear to have increased over time, and recently have been the dominant species in up to 80% of vegetation plots surveyed (D. Olson, pers. comm.). Squires and Anderson (1995) reported that swans avoided eating these species. Further, muskrat lodges historically were very important nest sites for swans (e.g., Banko 1960, Page 1976). Although quantitative data are unavailable, the general impression from biologists is that the abundance of lodges has decreased over time at Red Rock Lakes NWR. A water control structure was improved in the late 1980s, and has maintained water levels at the refuge's Lower Lake at fairly stable levels. If the refuge lakes and marshes function similarly to those in prairie ecosystems, these stable water levels likely could decrease the productivity of the system (e.g., Kantrud et al. 1989), and the apparent changes in vegetation and muskrat activity are consistent with that hypothesis. Yet, few of those who voice concern about the status of tri-state swans mention issues related to habitat management at Red Rock Lakes NWR or elsewhere as potential factors influencing swan status.

Although marking programs can be very valuable, several assumptions must be met to draw valid inferences (Brownie et al. 1985). In the case of trumpeter swans, we submit that marked samples may not adequately represent the groups to which inferences may be applied, and that differences in observer effort and coverage over time make conclusions tenuous. We note that the majority of the studies do not report the amount of observer effort, yet authors attempt to draw strong inferences from the results. For example, the contention has been made, based on neck-collar observations, that the Canadian and U.S. nesting birds are reproductively isolated because birds have not been seen nesting on their non-natal nesting grounds. However, as we stated earlier, although many swans have been marked over the years, the sample size can be reduced greatly once data are appropriately screened. Further, many swans are marked but never seen again, or are seen only during the first few years after marking (e.g., Gale et al. 1987:286, Shea and Drewien 1999). Given that swans are long-lived, much of the data reflect only a small fraction of these birds' reproductive lifetime. The pragmatic decision is to deem all those birds which are no longer sighted as dead. But obviously, trumpeter swans inhabit many remote areas, and not all areas may be amenable to direct observations of birds. Nonetheless, those areas, and the chance that marked birds may inhabit them, should not be dismissed. In fact, one observation of a mixed-group (Canadian/tri-state) pairing has been documented, band-recovery information indicates 2 U.S.-nesting birds were sighted in Alberta, and 2 birds marked in Grande Prairie summered in the U.S (Gale et al. 293-294). We contend that these instances suggest some reproductive intermingling of the Canada and Tri-state Area flocks may be occurring, that gene flow is possible between the groups, and that sampling procedures may simply have been inadequate to detect much interchange to date. Recent advances in the use of satellite telemetry may allow a better understanding of the movements of trumpeter swans, and recently initiated genetics studies (Oyler-McCance and Quinn 2001) may provide a more scientific assessment of population delineations.

The genetic structure of the RMP and the degree of differentiation among various nesting components remains unresolved. Although several studies have been conducted, sample sizes generally have been small and the techniques used are dated; more refined procedures are

available. However, all previous studies suggest a low degree of genetic diversity in the RMP, and authors generally conclude that the RMP and its segments experienced population bottlenecks, where only a small sample of the ancestral genome is available for propagation. Coincidentally, the productivity of swans nesting in the tri-state area is low relative to other groups of swans (Banko 1960, Shea and Drewien 1999, D. Duncan, pers. comm.). Some authors speculate that low genetic diversity decreases the viability of tri-state swans. However, we note that genetic diversity had to be at least as low in the 1930s as it is today (fewer individuals existed, and the chance for mutations has increased as their numbers have grown), yet the abundance of the birds increased until the 1950s (albeit with the help of management activities). The relative stability in the abundance of swans nesting in the tri-state area during the 1950s-1980s may have been the result of reaching the carrying capacity of the landscape (Banko 1960), although this conclusion, too, is speculation.

Thus, we believe the degree to which genetics may play a role in status of RMP (and particularly tri-state) swans is uncertain. Possible results, however, include a decrease in fitness or inbreeding depression. A better understanding of the impacts of low heterozygosity in RMP swans could greatly benefit management decisions. For example, if inbreeding depression is occurring, the birds could be at an evolutionary dead end. In this case, management actions, however heroic, may not prevent their demise. The apparent management action would be to introduce new alleles into the group (i.e., from either PCP or IP birds). Marsolais and White (1997) suggested that the introduction of new alleles into a group of reintroduced trumpeter swans in Ontario might result in a more vigorous and adaptive genome. Clearly we need to better understand the genetic relationships among the various groups of trumpeter swans for better-informed management decisions.

The distribution of RMP swans in the winter continues to be a concern for the Service. The potential for swans to die in the event of sustained, severe winter weather in the tri-state region remains. However, we note that such an occurrence has been experienced only once in recent history, and estimates suggest only about 100 birds (of both Canadian and tri-state origin) died. Whether the tri-state birds ever exhibited a strong migratory tradition is subject to much debate (see Gale et al. 1987, U.S. Fish and Wildlife Service 2001). Some authors contend that migratory traditions were destroyed as the range of the trumpeter swan was constricted during the 1900s due to overexploitation, and that the only way to re-establish those paths is to curtail mortality of 'pioneers'. Others believe that birds nesting in the tri-state area never exhibited large migratory movements. We believe there simply is no empirical evidence to refute either contention, although both are possible hypotheses. Although knowledge of migration pathways may be taught to offspring by adults, it is not necessarily the only means by which pathways are developed. Nevertheless, the desire to establish more migratory pathways for RMP birds is shared by the Service (Schmidt 2000) and its partners (Pacific Flyway Subcommittee on Rocky Mountain Trumpeter Swans 1998, 2002). Unfortunately, despite intensive efforts by the Service and its partners to disperse trumpeter swans to areas outside their primary wintering sites in Idaho and establish new migratory pathways, generally the efforts have failed (Shea and Drewien 1999, Trost et al. 2000). Most birds that were captured and translocated to alternate wintering

sites were either known to be dead, or were not seen after a few years and presumed dead; only 30% were known to be alive (Shea and Drewien 1999:26). Drawing primarily on experience trying to alter migrations of geese, Trost et al. (2000) believed altering the migratory traditions of waterfowl by direct intervention (e.g., translocations) is difficult if not impossible, and has yet to be successfully accomplished for any population. However, Trost et al. (2000) argue that changes in winter distributions may occur naturally, noting a recent change in the distribution of Cackling Canada geese, although the landscapes must be available to support them. Bouffard (2000) noted that the distribution of trumpeter swans wintering in the tri-state area have shifted southward in recent years, possibly in response to various management actions and pressure by an increasing population to seek alternative sites.

Due to the relative lack of success with winter-translocation efforts, the Service believes a more effective approach is through 'augmentation', the placement of swans into suitable nesting habitat during the summer. The idea would be to place birds in potential nesting areas situated near suitable wintering habitats, yet distant enough from the primary RMP wintering areas to decrease the possibility they would winter sympatrically with the bulk of the RMP. Although perhaps not stated explicitly in earlier efforts, the establishment of nesting flocks in the mid-1900s in other regions of the western U.S. using tri-state birds and eggs were the earliest expression of this management concept. By placing tri-state birds in various regions to establish new nesting flocks, the possibility of a catastrophic event extirpating the tri-state genome is extremely unlikely, thereby ensuring their continued existence. That is, the birds in these different regions (e.g., Nevada, Oregon, and High Plains flocks) are derived from tri-state genetic stock, but don't inhabit the tri-state area. In fact, the tri-state area may not be able to support more swans if habitat is limited, as some have suggested (e.g., Banko 1960). However, if the Oregon, Nevada, and High Plains restoration flocks are genetically similar to the extant tri-state birds from which they were derived, and can be considered 'tri-state birds', management has arguably succeeded in enhancing the status of tri-state birds by increasing the spatial range of the tri-state genome and increasing their abundance to levels above those observed historically.

We believe that, despite the relatively large volume of information collected over the years, much of that data does not allow for a rigorous testing of alternative hypotheses. Because of this, strong inferences about the movements, vital rates, and population dynamics of RMP swans are not possible. Thus, we contend that we understand much less about trumpeter swans than some authors believe. Because the Service is committed to making management decisions based on the best available science, it has in the past and will continue to support various programs for trumpeter swans, including those nesting in the tri-state area. The following list, although not exhaustive, describes some of these activities and the commitment by the Service to enhance the status of trumpeter swans:

1) Various banding/marking efforts to better understand vital rates
2) Annual surveys of the RMP (all flocks) during fall and mid-winter
3) The range-wide 5-year survey of all trumpeter swans
4) Ongoing swan-management activities on refuges

5) Protection, restoration, monitoring and research activities described in several plans
   a) Pacific Flyway's Trumpeter Swan Implementation Plan
   b) Draft Refuge Concept Plan for Trumpeter Swan Management
   c) Pacific Flyway Management Plan for RMP Trumpeter Swans
   d) Comprehensive Conservation Plans for various refuges
6) Wyoming Wetland Society's captive propagation activities
7) Egg and cygnet salvage operations
8) Monitoring of trumpeter swan take during Pacific Flyway general swan seasons
   a) operation of check station at Bear River Migratory Bird Refuge
   b) development of Memorandum of Understanding with the state of Utah that requires hunter education designed to limit take of trumpeters
9) Monetary support for winter swan surveys in Utah
10) Cooperative habitat projects within the Bridger-Teton, Targhee, and Caribou National Forests, Grand Teton National Park, and private lands
11) Winter translocations to the lower Bear River
12) Summer augmentations to various sites (e.g., Seedskadee NWR)
13) Salt River range-expansion project
14) Flathead Indian Reservation translocation project
15) Maintenance of the neck collar database by the Southeastern Idaho Refuge Complex
16) Swan and habitat research at Red Rock Lakes NWR
17) Monetary support for the trumpeter swan genetics study
18) Satellite- and radio-telemetry studies at Red Rock Lakes NWR and elsewhere

Finally, although the various individuals and groups arguing that the Tri-state Area flocks should be listed as a distinct population segment sincerely believe their actions will benefit swans, ironically, the opposite may be occurring. The Service often collaborates with state wildlife agencies to coordinate and conduct management programs for swans. However, the current litigation has concerned several states, who have decided not to promote trumpeter swan reintroduction or enhancement activities or suggest that current funding for swan programs may be curtailed, pending the outcome of the litigation (U.S. Fish and Wildlife Service 2001:43-44, B. Bales, Oregon Dept. of Fish and Wildlife, pers. comm.).

Fig. 1. Approximate nesting ranges of trumpeter swan populations (from Caithamer 2001).

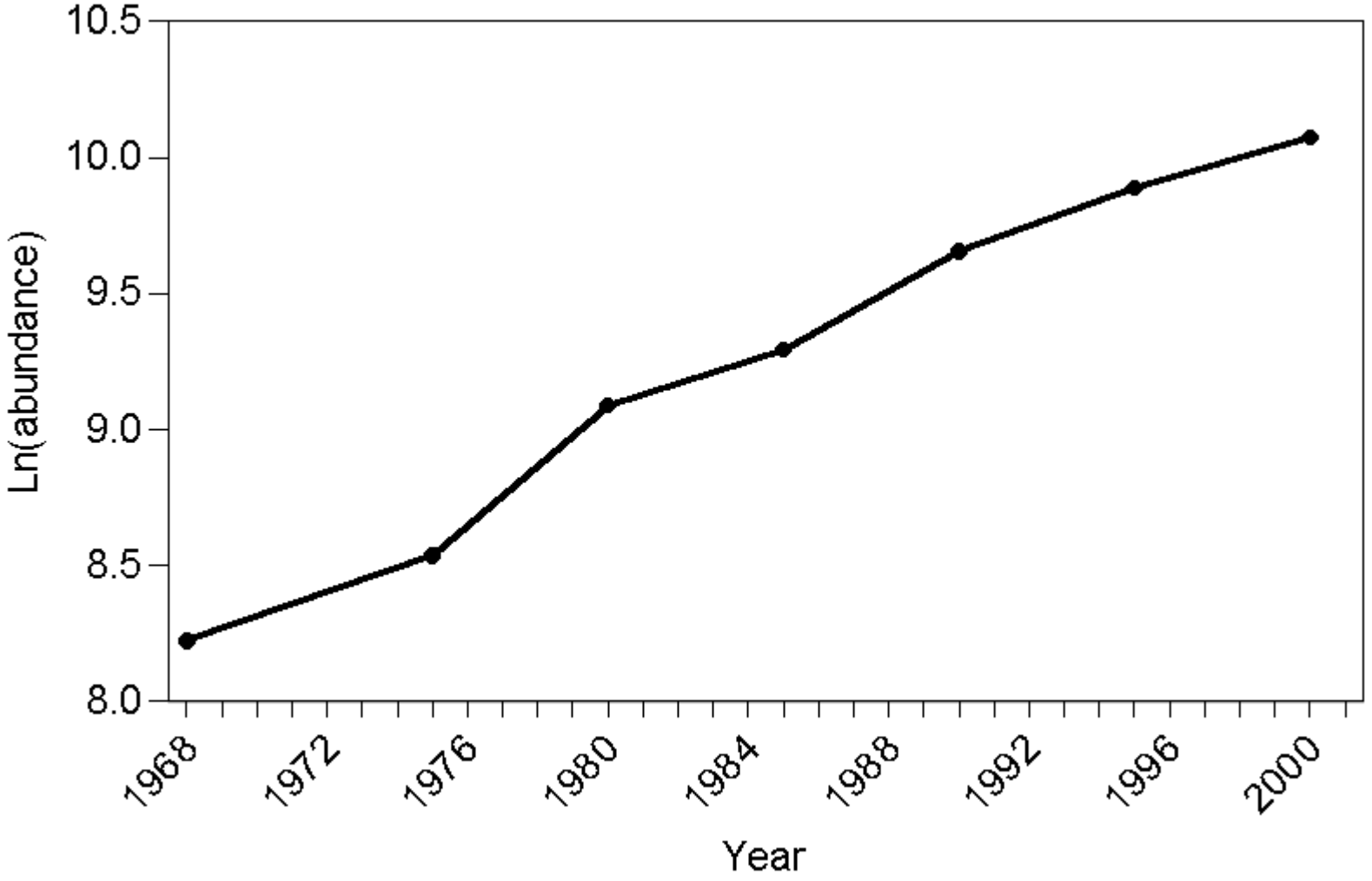

Fig. 2. Growth in abundance of trumpeter swans in North America, 1968-2000 (data from Caithamer 2001).

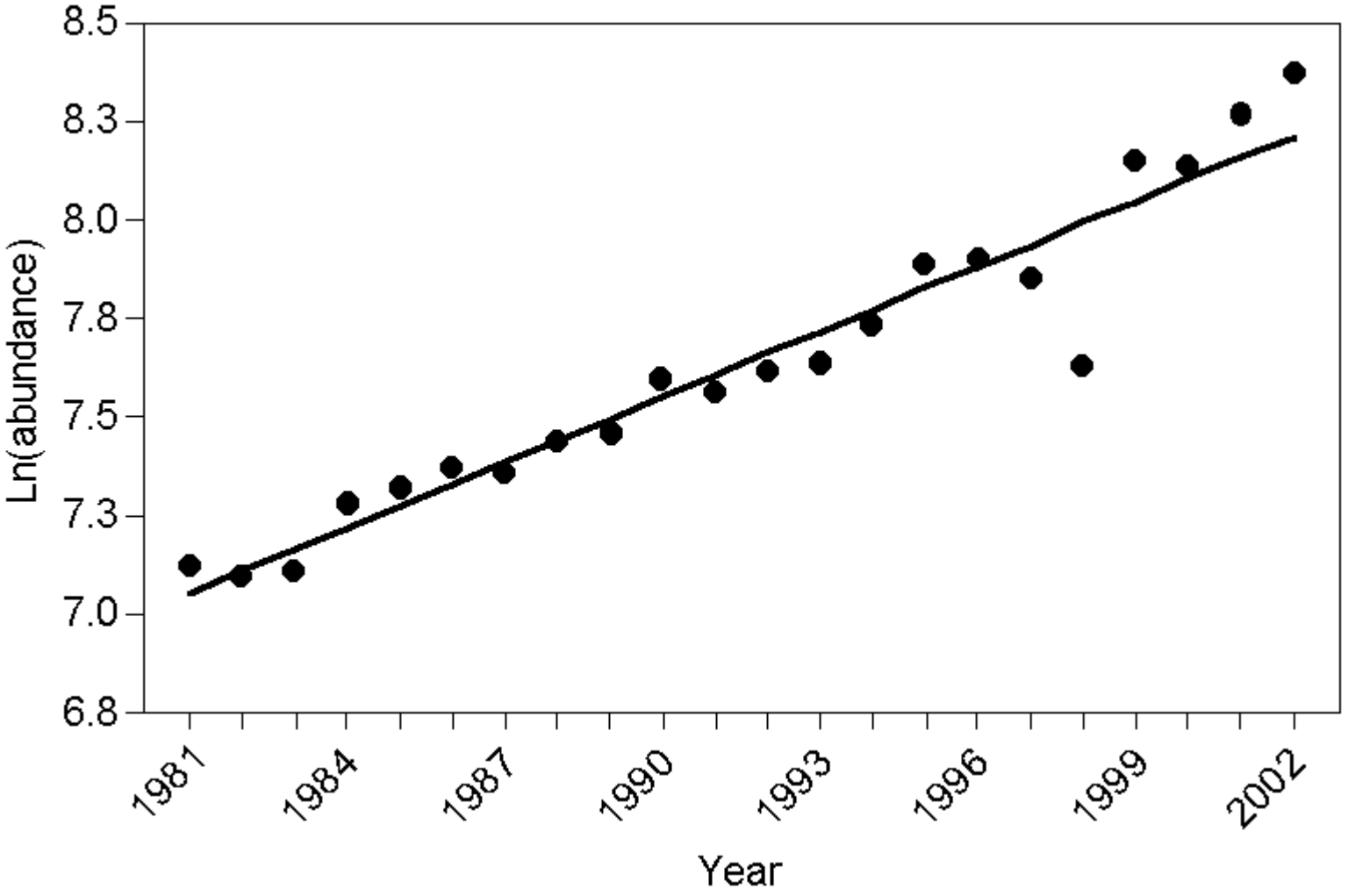

Fig. 3. Growth in abundance of Rocky Mountain Population trumpeter swans, 1981-2002, as measured by the mid-winter surveys.

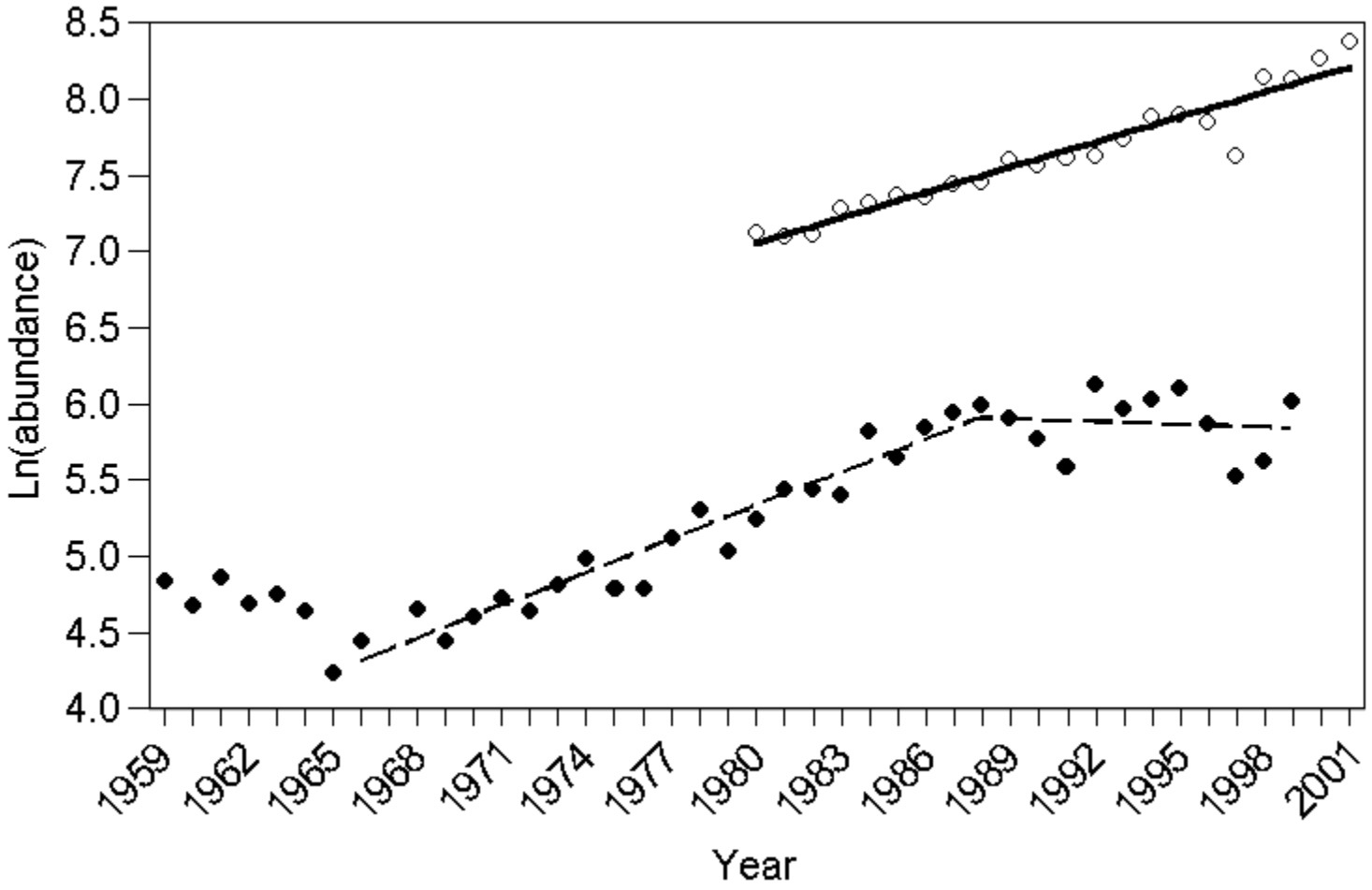

Fig. 4. Growth of the Canada flocks of Rocky Mountain Population trumpeter swans, as measured by counts of the Grande Prairie birds (solid circles and dashed line) and the difference between the mid-winter and fall surveys in the tri-state region (open circles and solid line).

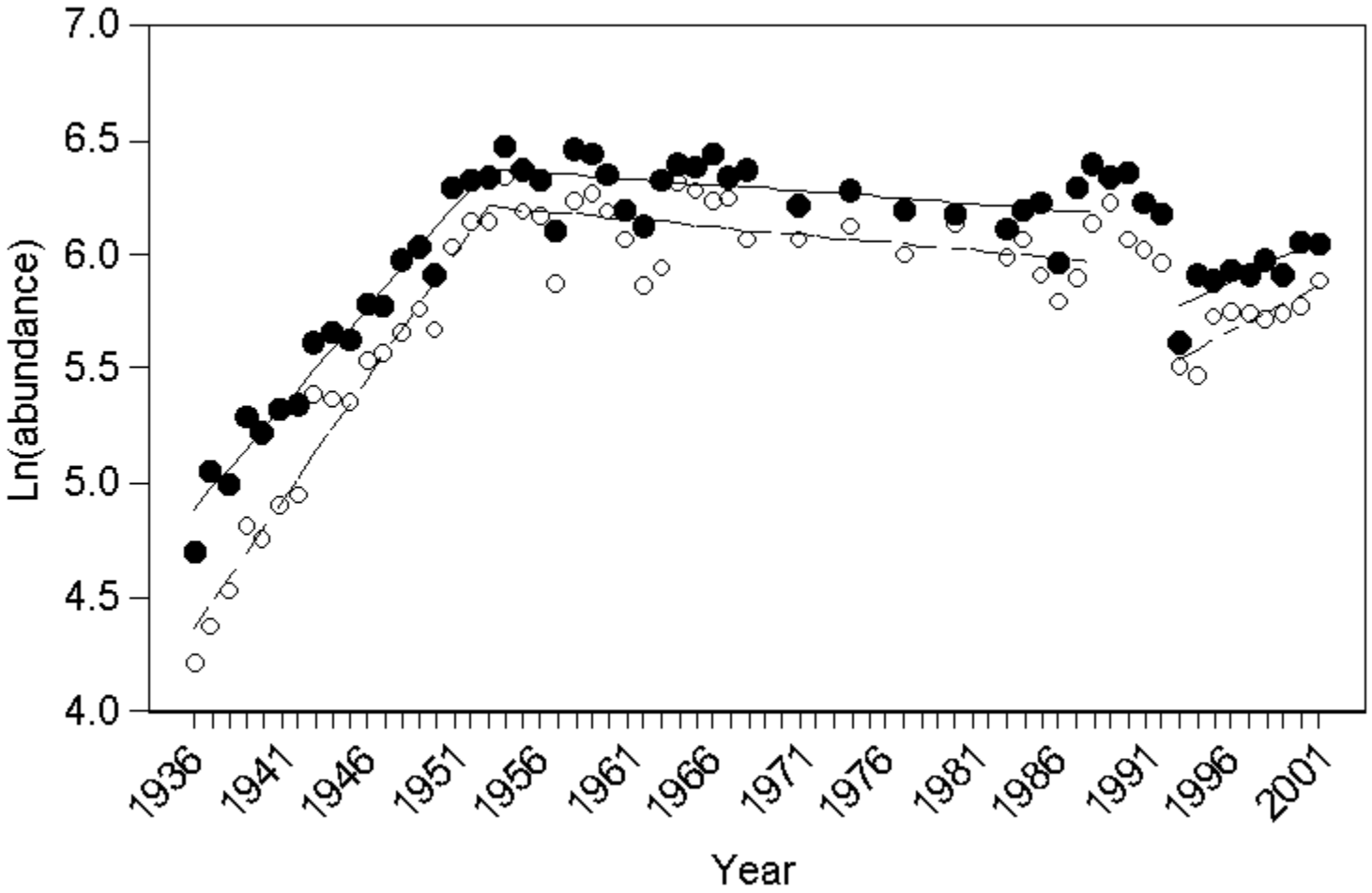

Fig. 5. Piecewise regression for log-transformed counts of trumpeter swans in Tri-state Area flocks, 1936-88, and simple linear regression for log-transformed counts during 1993-2001. Solid circles and lines denote all birds; open circles and dashed lines denote only white birds (i.e., adults and subadults).

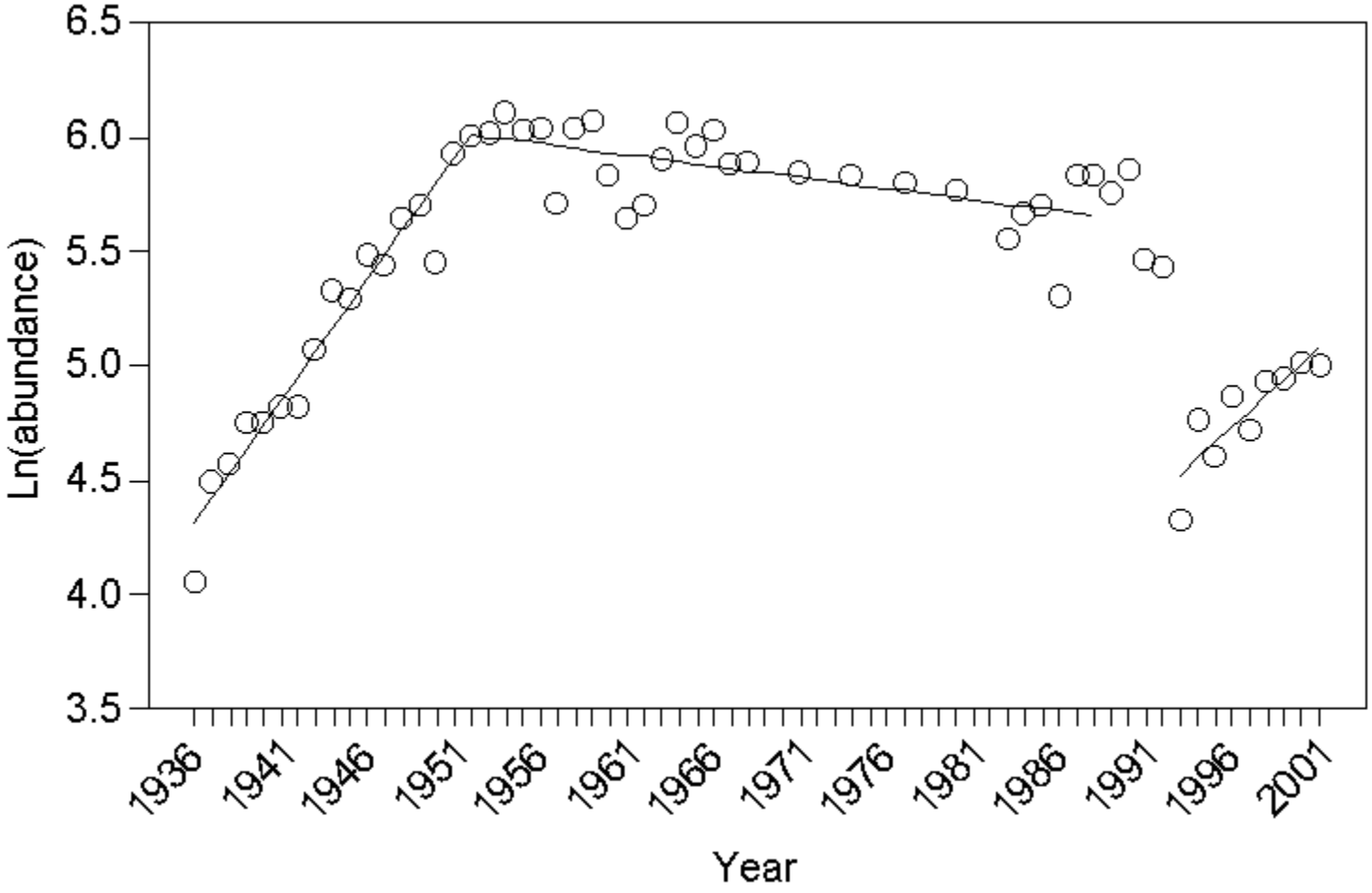

Fig. 6. Piecewise regression for log-transformed counts of nesting trumpeter swans in Montana, 1936-88, and simple linear regression for log-transformed counts during 1993-2001.

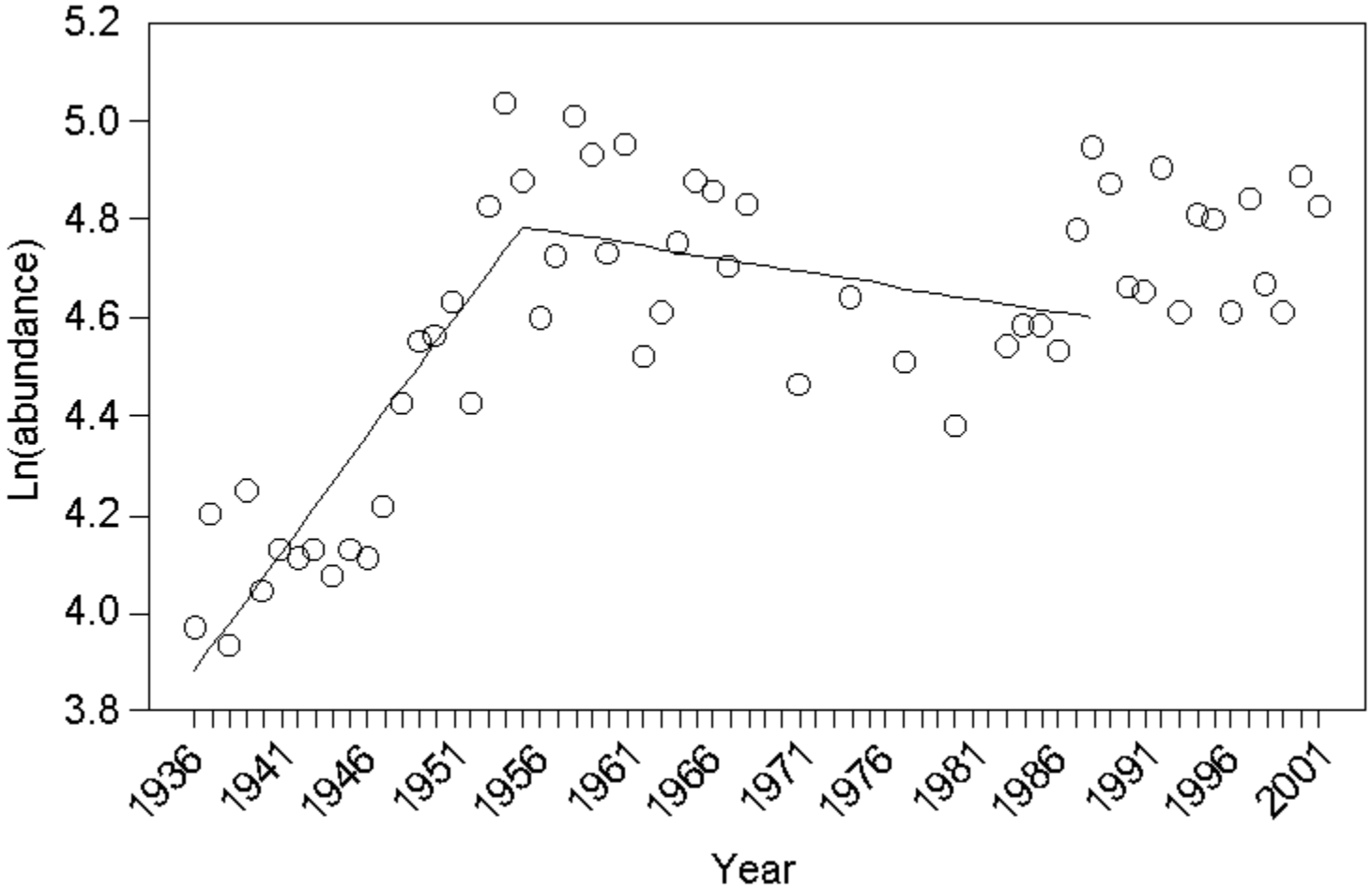

Fig. 7. Piecewise regression for log-transformed counts of nesting trumpeter swans in Wyoming, 1936-88, and simple linear regression for log-transformed counts during 1993-2001.

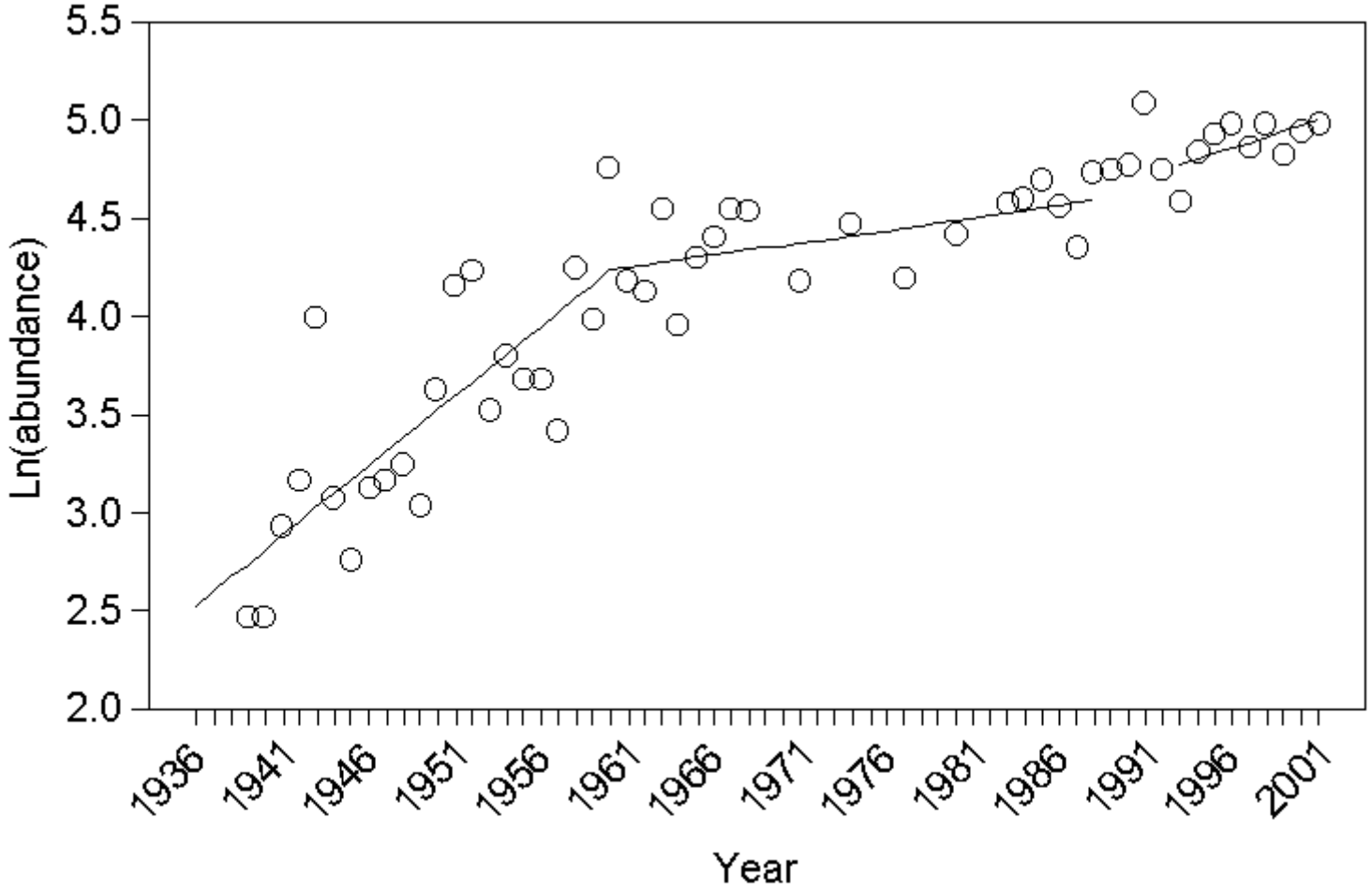

Fig. 8. Piecewise regression for log-transformed counts of nesting trumpeter swans in Idaho, 1936-88, and simple linear regression for log-transformed counts during 1993-2001.

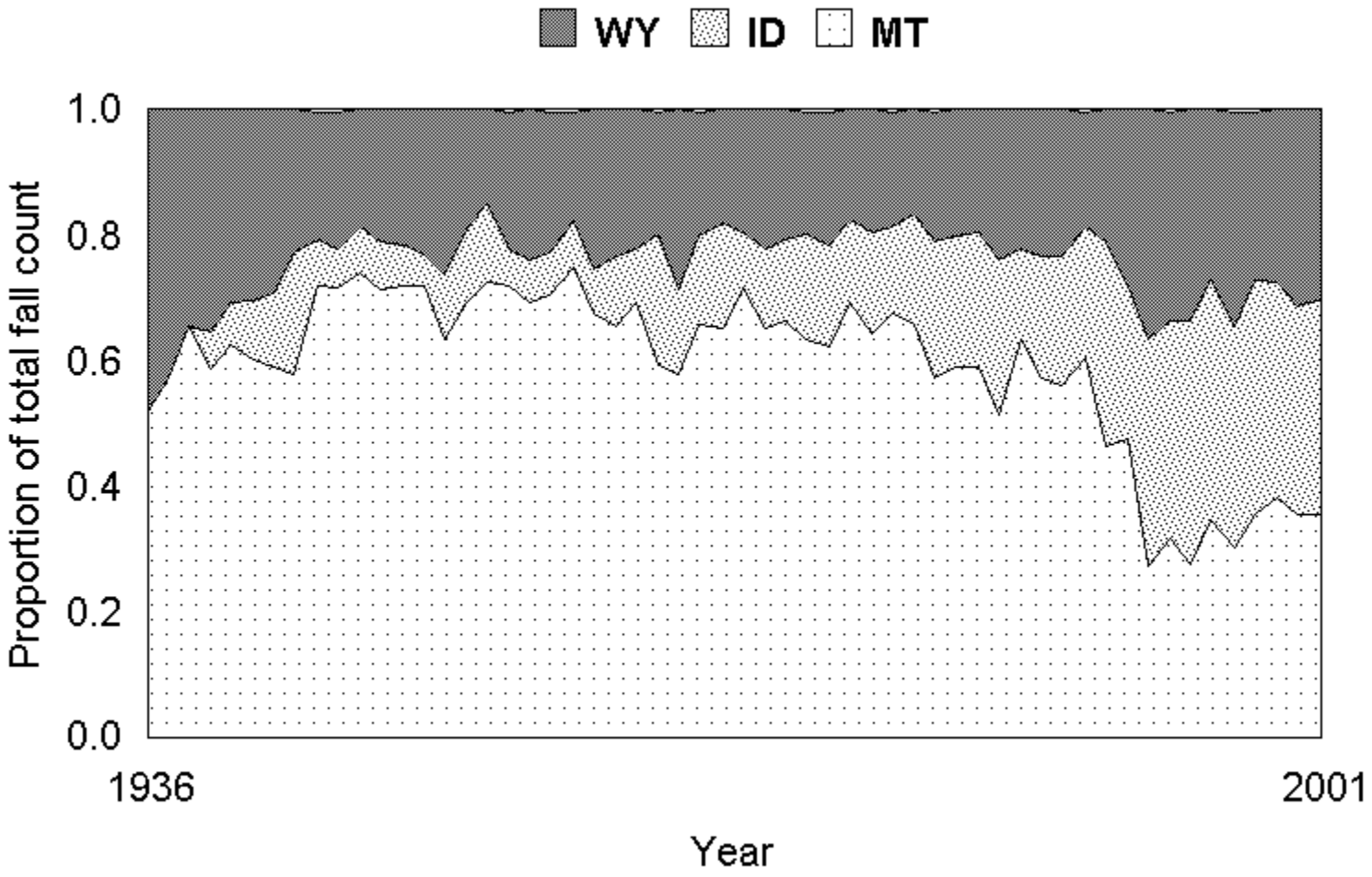

Fig. 9. Proportion of swans from Tri-state Area flocks counted in Idaho, Montana, and Wyoming during the annual fall surveys.

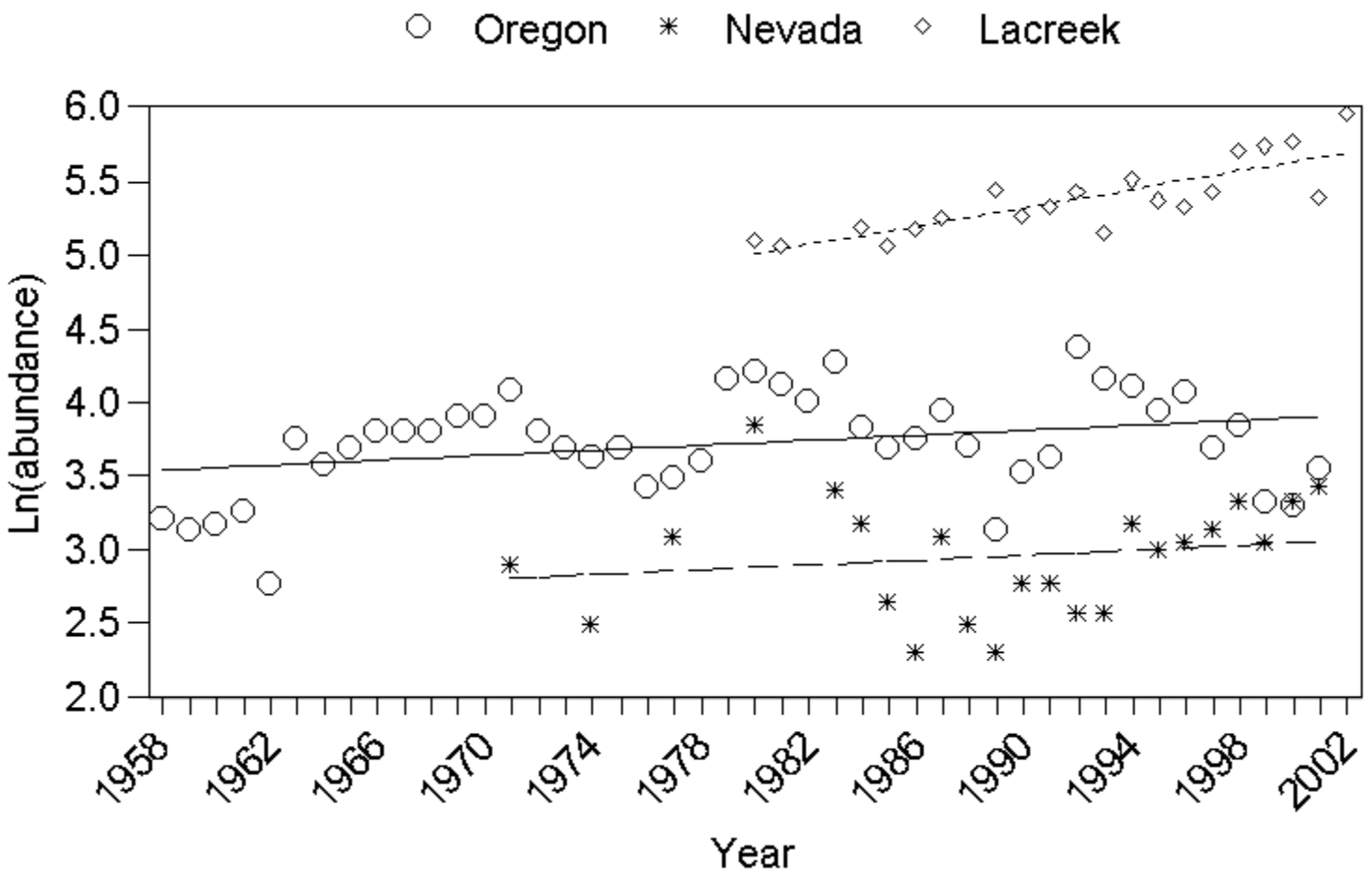

Fig. 10. Linear regression for log-transformed counts of Oregon, Nevada, and High Plains nesting flocks of trumpeter swans.

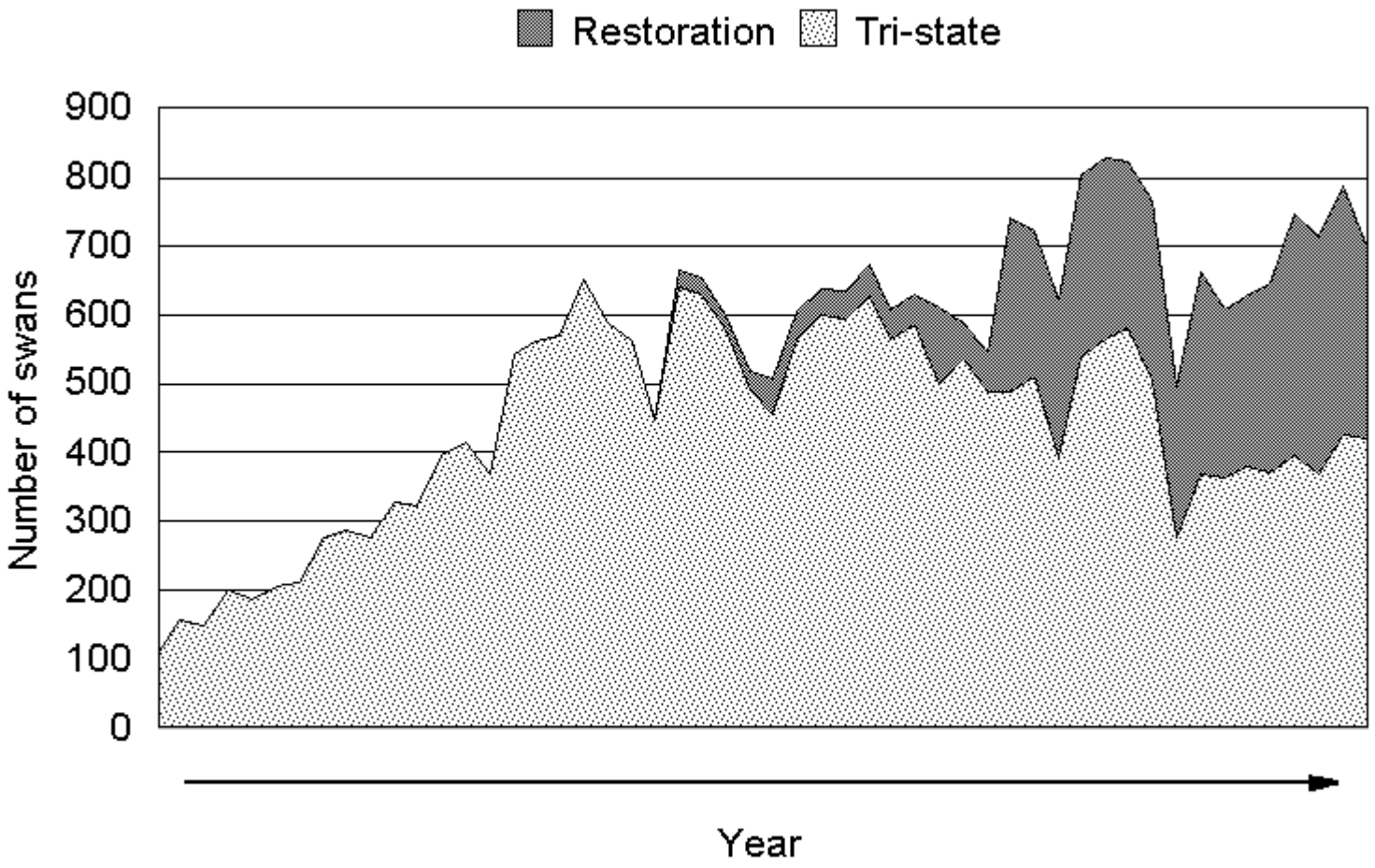

Fig. 11. Fall counts of swans in Tri-state Area flocks and those from restoration flocks (Oregon [less counts from Summer Lake WMA and vicinity], Nevada, and High Plains flocks).

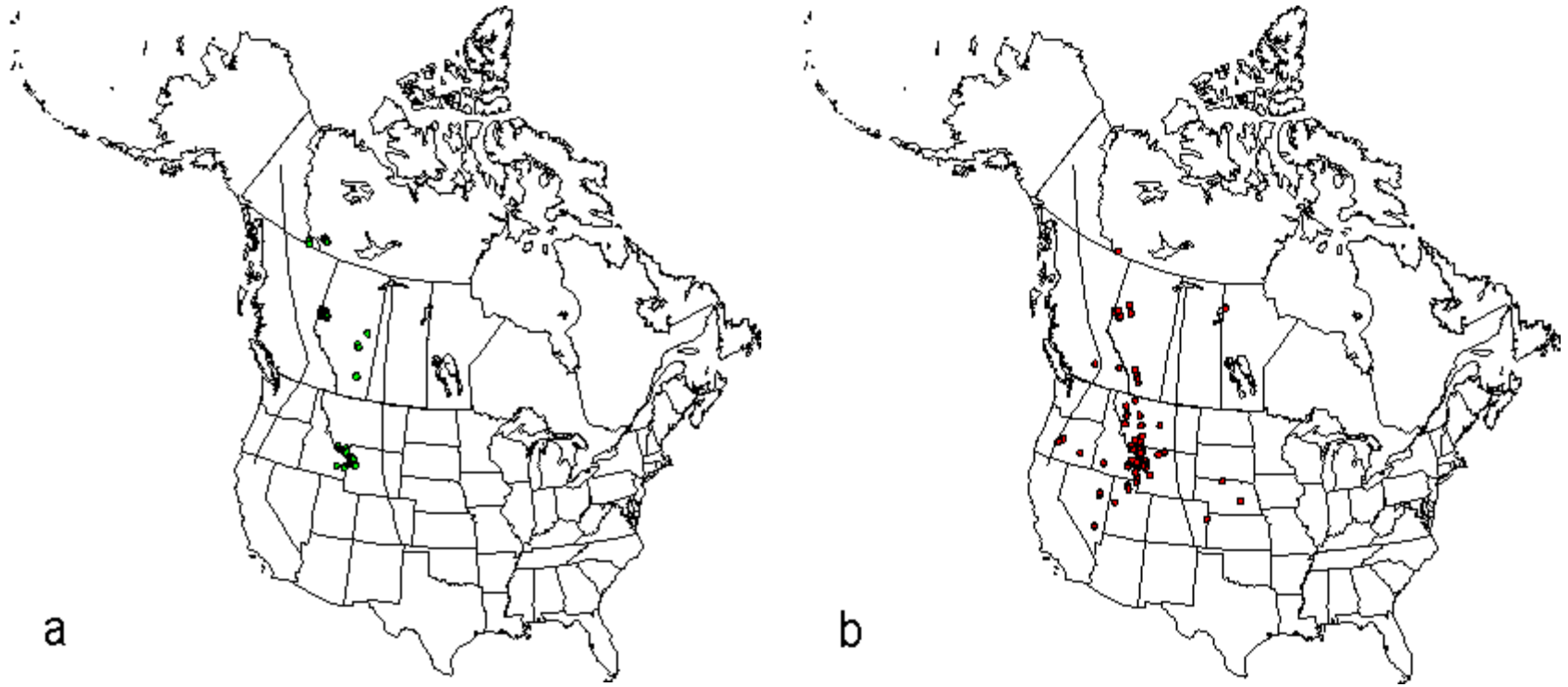

Fig. 12. Distributions of 1,971 trumpeter swans banded during 1949-98 (a) and subsequent resightings (315) of those banded birds (b).

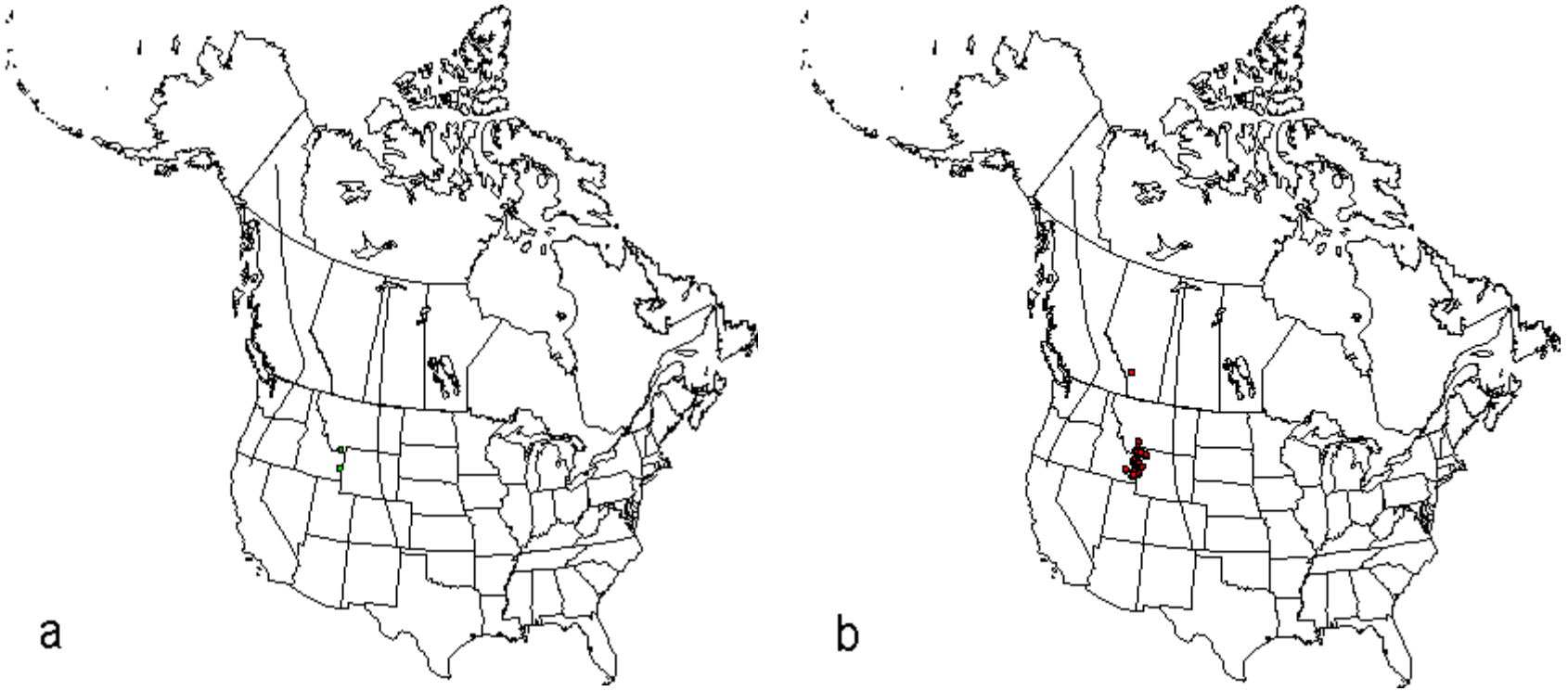

Fig. 13. Distributions of 157 trumpeter swans marked with neck collars during 1988-2002 (a) and subsequent resightings (1,563) of those marked birds (b).

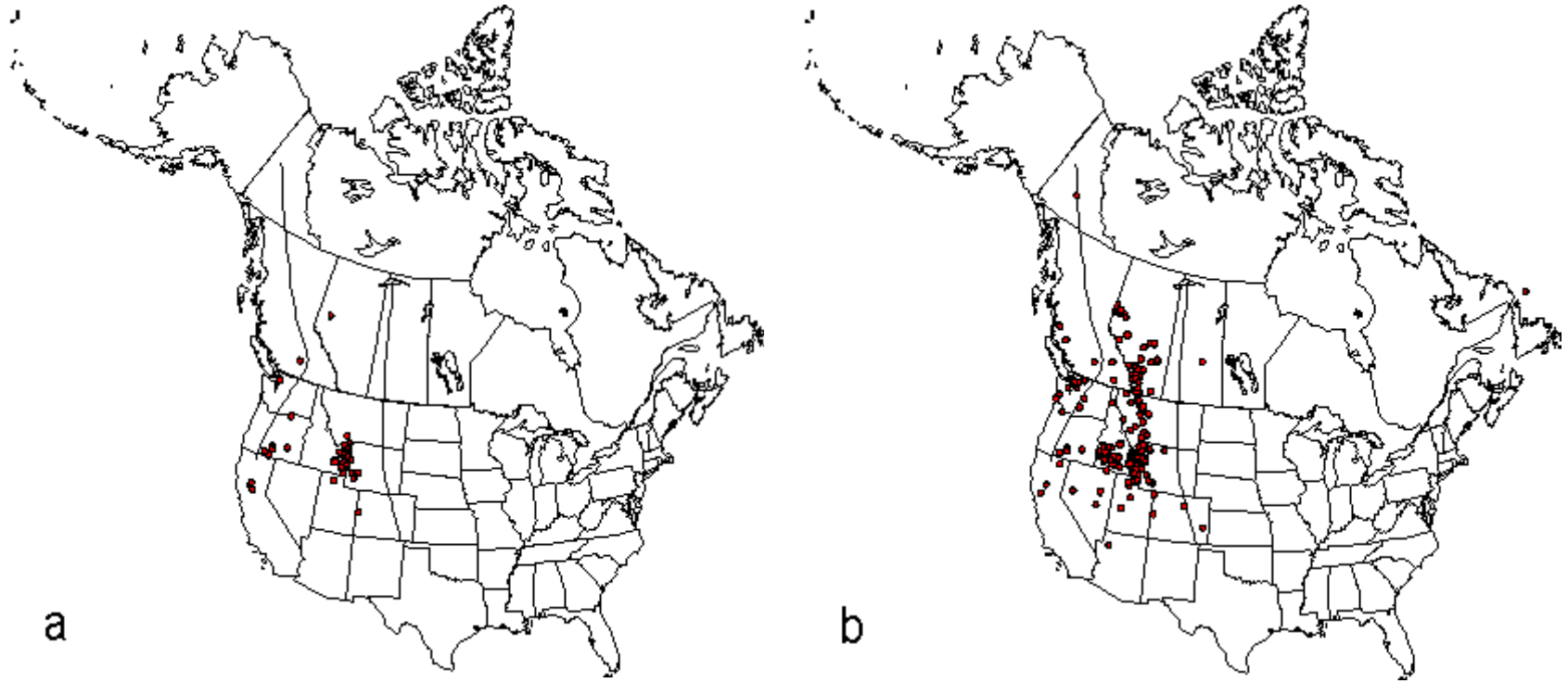

Fig. 14. Distributions of (a) trumpeter swans captured and marked with neck collars during summer and translocated to a new release site during 1988-2002, and (b) swans captured and marked with neck collars during winter and translocated to a new release site, 1998-2002.

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